

# Nighttime sap flow of *Acacia mangium* and its implications for nighttime transpiration and stem water storage

Hua Wang<sup>1,2,3</sup>, Ping Zhao<sup>1,\*</sup>, Dirk Hölscher<sup>4</sup>, Quan Wang<sup>5</sup>,  
Ping Lu<sup>6</sup>, Xi A. Cai<sup>1</sup> and Xiao P. Zeng<sup>1</sup>

<sup>1</sup> South China Institute of Botany, Chinese Academy of Sciences, Guangzhou 510650, China

<sup>2</sup> Institute of Forestry and Pomology, Beijing Academy of Agriculture and Forestry Sciences, Beijing 100093, China

<sup>3</sup> Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing 100085, China

<sup>4</sup> Department of Tropical Silviculture and Forest Ecology, University of Göttingen, 37077 Göttingen, Germany

<sup>5</sup> Faculty of Agriculture, Shizuoka University, Shizuoka 422-8529, Japan

<sup>6</sup> Energy Resources of Australia Ltd, GPO Box 2394, Darwin, Northern Territory, 0801, Australia

\*Correspondence address. South China Institute of Botany, Chinese Academy of Sciences, Guangzhou 510650, China. Tel: +0086-20-37252881; Fax: +0086-20-37252831; E-mail address: zhaoping@scib.ac.cn

## Abstract

### Aims

Nighttime sap flow of trees may indicate transpiration and/or recharge of stem water storage at night. This paper deals with the water use of *Acacia mangium* at night in the hilly lands of subtropical South China. Our primary goal was to reveal and understand the nature of nighttime sap flow and its functional significance.

### Methods

Granier's thermal dissipation method was used to determine the nighttime sap flux of *A. mangium*. Gas exchange system was used to estimate nighttime leaf transpiration and stomatal conductance of studied trees.

### Important Findings

Nighttime sap flow was substantial and showed seasonal variation similar to the patterns of daytime sap flow in *A. mangium*. Mean nighttime sap flow was higher in the less precipitation year of 2004 (1122.4 mm) than in the more precipitation year of 2005 (1342.5 mm) since more daytime transpiration and low soil water availability in the relatively dry 2004 can be the cause of more nighttime sap flow. Although vapor pressure deficit and air temperature were significantly correlated with

nighttime sap flow, they could only explain a small fraction of the variance in nighttime sap flow. The total accumulated water loss ( $E_L$ ) by transpiration of canopy leaves was only ~2.6–8.5% of the total nighttime sap flow ( $E_t$ ) during the nights of July 17–18 and 18–19, 2006. Therefore, it is likely that the nighttime sap flow was mainly used for refilling water in the trunk. The stem diameter at breast height, basal area and sapwood area explained much more variance of nighttime water recharge than environmental factors and other tree form features, such as tree height, stem length below the branch, and canopy size. The contribution of nighttime water recharge to the total transpiration ranged from 14.7 to 30.3% depending on different DBH class and was considerably higher in the dry season compared to the wet season.

**Keywords:** heat dissipation method • nighttime sap flow • nighttime leaf transpiration • stem water recharge

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## INTRODUCTION

Due to ever-growing intense human activities, the earth's surface has warmed up by >0.8°C over the past century and by approximately 0.6°C in the past three decades (NASA 2007). In northern latitudes, night temperatures increased

more than day temperatures in the 20th century (Folland *et al.* 2001). Unless atmospheric humidity increases as well, this may lead to an elevated evaporative demand on some tree species at night, which may in turn alter the diurnal balance of forest water use (Daley and Phillips 2006). Therefore, it is essential to increase our knowledge concerning the water use of

forest trees at night. With the help of the sap flow measurement, a growing number of studies have recently revealed previously unknown information on nighttime water use in different forest tree species (Dawson *et al.* 2007; Fisher *et al.* 2007; Goldstein *et al.* 1998; Marks and Lechowicz 2007; Zeppel *et al.* 2010).

Nighttime sap flow is defined as the stem sap flux when solar radiation was less than  $5.0 \text{ W m}^{-2}$ . It could either be a result of actual nighttime transpiration of the canopy (Benyon 1999) or of recharging the depleted internal water storage of trees (Caspari *et al.* 1993; Daley and Phillips 2006; Lu *et al.* 1995) or both. Daytime canopy transpiration causes a deficit in the internal water storage of trees that can primarily be recharged through nighttime sap flow. As a commonly occurring physiological activity, nighttime sap flow has the following physiological benefits for plants: (i) nighttime sap flow delivers available and mobile N to the roots and transports it rapidly upwards, thus partially compensating for declines in plant N content under  $\text{CO}_2$  enrichment (McDonald *et al.* 2002); (ii) nighttime sap flow helps to recover hydraulic conductance from partial xylem cavitation that might occur during stressful daytime conditions (Snyder *et al.* 2003) and (iii) nighttime sap flow assures an earlier resumption of higher transpiration and photosynthetic rates in the following morning (Daley and Phillips 2006), as well as avoiding lags between assimilation and increased stomatal conductance (Oren *et al.* 2001). Although water stored in plant tissues is potentially important for the regulation of water consumption of canopy trees, limited information on the contribution of internal water recharge to the total water consumption is available (Goldstein *et al.* 1998).

*Acacia mangium* is a medium-sized, evergreen tree species with phyllodes that serve as leaves (Sá *et al.* 1999). This tree species is planted throughout the humid tropics (Turnbull 1986) and has become naturalized in subtropical China since the late 1970s. Due to its fast growth rate and nitrogen fixation capacity, it has been commonly used as a pioneer species for vegetation restoration, especially in the hilly lands of subtropical China (Zhao *et al.* 2002, 2006). It can be expected that water use is crucially important in supporting the intensive growth rate of *A. mangium*. In consideration of the simplicity, high degree of accuracy and reliability, and relatively low cost of the Granier's thermal dissipation probe (TDP) method (Lu *et al.* 2004), we applied TDP to measure the nighttime sap flow of *A. mangium* and analyze its correlates with possible driving factors. Our primary goals of this study were (i) to analyze the characteristics of nighttime sap flow and its environmental dependence, (ii) to reveal and understand the nature of nighttime sap flow and its functional significance, and (iii) to evaluate nighttime stem water recharge and its implications for the total daily transpiration.

## MATERIALS AND METHODS

### Site description

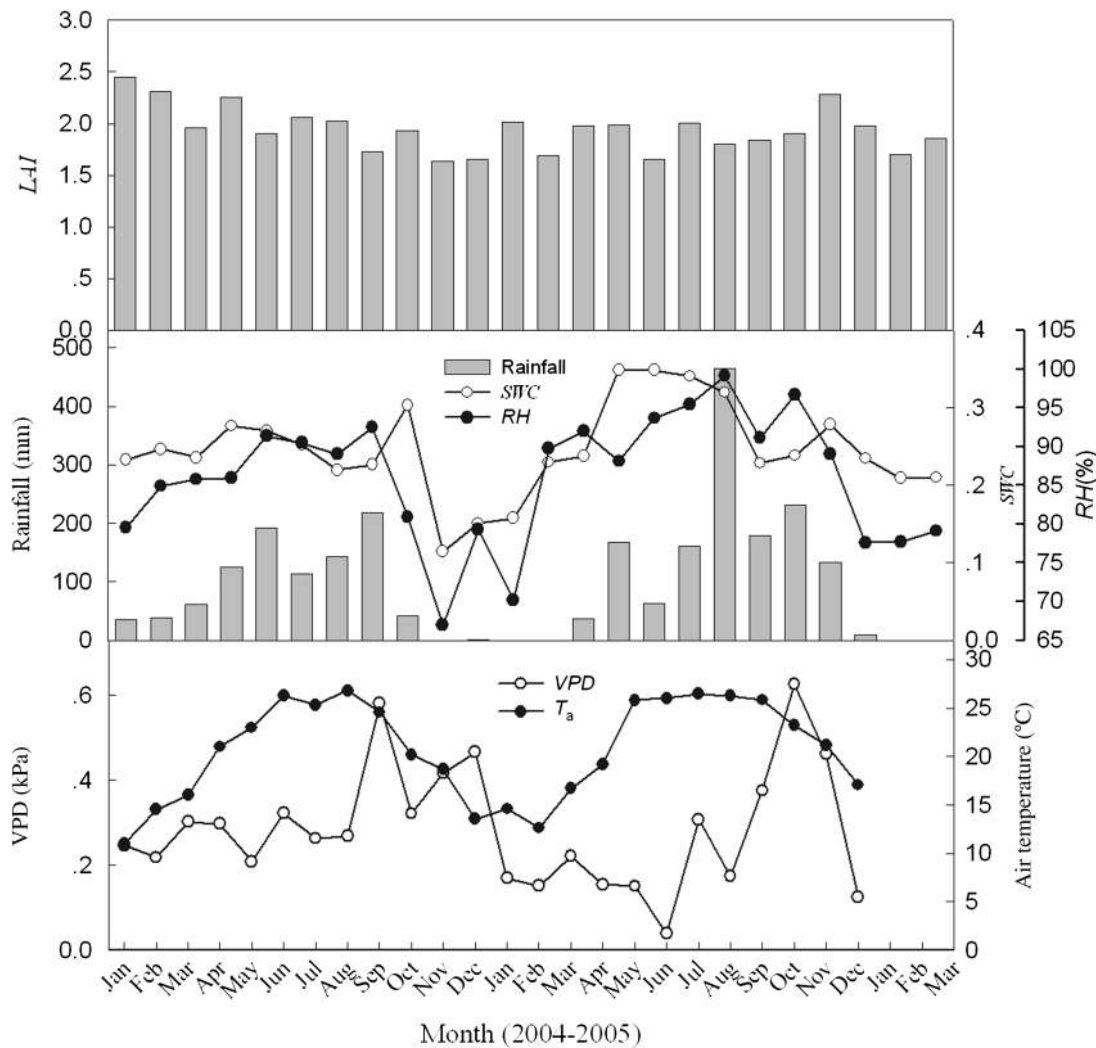
This field study was conducted in the consecutive years of 2004 and 2005 in an *A. mangium* plantation in the Heshan Hilly

Land Interdisciplinary Experimental Station ( $112^{\circ}53'15''$ – $112^{\circ}54'00''\text{E}$ ,  $22^{\circ}40'07''$ – $22^{\circ}41'07''\text{N}$ ), Guangdong Province, China. An experimental plot with an area of  $640.5 \text{ m}^2$  ( $36.6 \times 17.5 \text{ m}$ ) was set up in the mature *A. mangium* plantation. The 19-year-old stand was planted with a spacing of  $3 \times 3 \text{ m}$  and is considered to be in its declining stage. There is slight defoliation from December to February in the following year. The plot comprised 47 trees (734 trees per hectare) with a basal area of  $26.6 \text{ m}^2 \text{ ha}^{-1}$ . Tree height ranged from 2.4 to 22.8 m with an average of 15.7 m. Stem diameter at breast height (DBH) was between 3.8 cm and 37.5 cm with an average of 20.1 m. Canopy size was estimated to range from 0.8 to  $53.0 \text{ m}^2$  with an average of  $13.8 \text{ m}^2$ , assuming it to be an ellipse. Thirteen selected trees for sap flow measurement gave a representative range of sizes with tree height ranging from 12 to 22.8 m, DBH between 13.4 and 37.5 cm and canopy size ranging from 4.6 to  $47.7 \text{ m}^2$ .

The stand grows on a slope with lateritic soil at an elevation of  $\sim 80 \text{ m}$  above sea level. Annual mean temperature is  $21.7^{\circ}\text{C}$  with the monthly minimum in January ( $13.1^{\circ}\text{C}$ ) and the monthly maximum in July ( $28.7^{\circ}\text{C}$ ). The study site receives an annual mean radiation of  $4.35 \times 10^5 \text{ W}\cdot\text{cm}^{-2}$  (Zhao *et al.* 2006). Precipitation ( $1333 \text{ mm}$  per year, averaged from the period of 2000–2006) in the area is unevenly distributed throughout the year with approximately 78% of the annual total occurring from March to September. The average volumetric soil water content (SWC) at the study site in 2004 was 0.24 and  $0.23 \text{ m}^3\cdot\text{m}^{-3}$  during the day and the night, respectively, and in 2005, it was 0.31 and  $0.30 \text{ m}^3\cdot\text{m}^{-3}$ , respectively. During the wet season, the average SWC was  $0.26 \text{ m}^3\cdot\text{m}^{-3}$  in 2004 and  $0.30 \text{ m}^3\cdot\text{m}^{-3}$  in 2005, while during the dry season (October to February) it was  $0.18 \text{ m}^3\cdot\text{m}^{-3}$  in 2004 and  $0.22 \text{ m}^3\cdot\text{m}^{-3}$  in 2005 (Fig. 1).

### Sap flow measurement

Thirteen sample trees of *A. mangium* from different DBH classes were selected for the measurements of sap flow. The DBH rank of the thirteen sample trees was  $<15 \text{ cm}$  (no. 13),  $15$ – $20 \text{ cm}$  (no. 5, 7, 11, 12, 14),  $20$ – $25 \text{ cm}$  (no. 2, 8, 9),  $25$ – $30 \text{ cm}$  (no. 1, 10) and  $>30 \text{ cm}$  (no. 3, 4). Xylem sap flux density expressed on a sapwood area basis was measured by means of self-made Granier-type sap flow sensors that were installed inside the stem sapwood at breast height (1.3 m above ground) (Granier 1987; Lu *et al.* 2004; Zhao *et al.* 2005). The sensors consist of two 2-cm-long probes, each containing a copper-constantan thermocouple. The constantan ends of the two thermocouples are connected to measure the temperature difference between the two probes. The probes were inserted vertically into the trunk with one located 10 cm above the other. The upper probes were continuously heated with a constant power of 0.2 W, while the lower probes were left unheated to measure the ambient temperature of the wood tissue and to act as a reference (Granier 1987). Four pairs of probes were installed on four sides of samples tree 1, 2, 3 and 4. One pair of probes was applied on the northern side of stem of the other nine trees. The sensors and adjacent portions of stem were wrapped with plastic insulation to protect the probes from



**Figure 1:** monthly average LAI of the *Acacia mangium* stand, rainfall, air relative humidity (RH), soil water content (SWC) at a soil depth of 30 cm, ambient temperature ( $T_a$ ) and the mean daytime vapor pressure deficit (VPD) for the study period.

mechanical damage, and the entire assembly was enclosed in an outer layer of aluminum film in order to minimize spurious temperature gradients caused by radiant heating of the stem, as well as to protect against water running down the trunk (Zhao *et al.* 2005). Sap flux density ( $J_s$ ,  $\text{g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) was calculated from the temperature difference using Granier's (1987) empirical relationship:

$$J_s = 118.99 \times \left( \frac{\Delta T_m - \Delta T}{\Delta T} \right)^{1.231} \quad (1)$$

In this equation,  $\Delta T_m$  is the temperature difference between the heated and the unheated probes when xylem sap flow is zero, which is computed with the Baseline program developed by Yavor Parashkevov in Nicholas School of Environment and Earth Sciences at Duke University, USA.  $\Delta T$  is the actual temperature difference between the two probes (Granier 1987). The data were sampled at interval of 30 s, averaged and recorded every 10 min by a Delta-T logger (DL2e,

UK). Continuously measured data were gathered beginning from August 2003 to the end of 2007. However, only original data from 2004 and 2005 and partial data from July 2006 were used for the analyses in this study.

### Environmental monitoring and leaf area index measurements

Volumetric soil water content (SWC,  $\text{m}^3\cdot\text{m}^{-3}$ ) at the study site was measured using three soil moisture probes (ML2x; Delta-T Device, UK) in the upper mineral soil (0–30 cm) amongst the selected trees. Photosynthetically active radiation (PAR,  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), air temperature ( $T_a$ ,  $^{\circ}\text{C}$ ), air relative humidity (RH, %) and wind speed ( $v$ ,  $\text{m}\cdot\text{s}^{-1}$ ) were monitored in a weather station located 150 m away from the study site.  $T_a$  and RH were measured using a HMP35E sensor (HMP35E; Vaisal, Finland). PAR was measured with a Li-cor quantum sensor. The meteorological data were sampled and recorded at the same frequency as sap flow measurements. We calculated vapor pressure deficit

(VPD, kPa) using the 10-min averages of temperature and RH according to Campbell and Norman (1998):

$$\text{VPD} = a \times \exp\left(\frac{bT}{T+C}\right) (1 - \text{RH}), \quad (2)$$

where  $a$ ,  $b$  and  $c$  are fixed parameters which are 0.611 kPa, 17.502 (unitless) and 240.97°C.

Measurements of stand leaf area index (LAI) using a CID Plant Canopy Analyzer (CID-110, USA) were undertaken under diffuse light conditions on cloudy days or at dusk, once a month from 2004 to 2005. The LAI of the *A. mangium* stand did not change apparently during the study period (Fig. 1). The average values of LAI in 2004 and 2005 were 2.00 and 1.89, respectively, and the difference between the 2 years was not significant ( $n = 12$ ,  $P = 0.364 > 0.05$ ). The slight decrease in LAI in 2005 may be due to slower growth under more rainy or cloudy weather condition in 2005.

### Estimation of the sapwood cross-sectional area

Twenty-three *A. mangium* trees in the surrounding area outside but close to the plot were randomly chosen and cores of 5 mm diameter were drilled out with an increment borer. Since the sapwood is easily distinguished from the heartwood, the sapwood thickness in the chosen trees was determined using a ruler on the fresh wood cores. We established the relationship between sapwood area ( $\text{cm}^2$ ) and DBH (cm) as follows:

$$A_s = m(\text{DBH})^n, \quad (3)$$

where DBH stands for diameter at breast height,  $m$  and  $n$  are coefficients by non-linear regression (0.1930 and 1.844). The formula was used to calculate the sapwood cross-sectional area of sample trees for the sap flow measurements, which is a key factor for calculating whole-tree transpiration. The characteristics of the 13 sample trees used for sap flow measurement had been published (Ma et al., 2008).

### Leaf gas exchange

Leaf transpiration and stomatal conductance of 27 healthy mature and fully expanded leaves from the inner and outer canopy of 3 middle-size and sun-exposed trees (9 leaves for each tree) within the experimental plot were measured with a gas exchange

system (LI-6400; Li-cor, USA). The measurements were taken on an hourly basis from 17:00 to 7:00 (GMT +08:00) on July 18–19 and 19–20, 2006. The purpose of these measurements was to confirm if there was obvious nighttime transpiration in *A. mangium*. Factors such as sun exposure and accessibility were taken into consideration during sampling. The twigs were pulled down to a certain height so that the leaves on the twigs could be conveniently accessed and measured with the Li-cor 6400.

### Calculation of nighttime sap flow and canopy leaf transpiration

The nighttime sap flow ( $E_n$ ) was calculated as follows:

$$E_n = \sum (J_s \times t) \times A_s, \quad (4)$$

where  $J_s$  is the sap flux density during the time period when solar radiation was less than  $5.0 \text{ W m}^{-2}$ ,  $t$  is 600 s (data were averaged and stored every 10 min in the logger) and  $A_s$  is the sapwood cross-sectional area ( $\text{cm}^2$ ). If the leaf transpiration of canopy comprises inappreciable fraction of the nighttime sap flow, we can assume that the nighttime sap flow is primarily used to recharge depleted internal water storages of trees, and  $E_n$  is nearly equal to nighttime stem water recharge ( $W_n$ ).

We roughly calculated the total water loss ( $E_L$ ) by leaf transpiration per tree by cumulating the hourly averaged measured transpiration rate ( $T_r$ ) and multiplying it by the total leaf area ( $A_L$ ).  $A_L$  of each tree was calculated from an established allometric equation ( $A_L = 0.2847 \text{ DBH}^{1.7535}$ ) based on unpublished data gathered in the same stand. The  $E_L$  is expressed as follows:

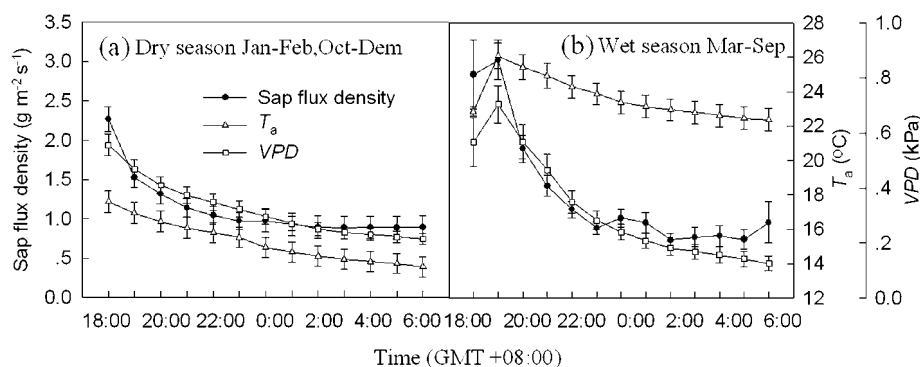
$$E_L = \sum (T_r \times t) (A_L). \quad (5)$$

In the equation,  $E_L$  is the nighttime leaf transpiration,  $t$  is 3600 s (data were measured every hour) and  $A_L$  is the total leaf area ( $\text{m}^2$ ).

### Statistical analyses

Statistical analyses were performed using SPSS 11.5 (SPSS Inc., Chicago, IL) and Sigmaplot 10.0 (Systat Software Inc., San Jose, CA). Data were presented as means  $\pm$  standard errors in Figs 2, 4, 6 and 8.

Paired  $t$ -test was performed to test whether there were significant differences between LAI in 2004 and 2005.



**Figure 2:** variation in mean nighttime sap flux density of 13 sample trees of *A. mangium*,  $T_a$  and VPD in dry and wet seasons of 2005.

Independent *t*-tests were conducted to test whether there were significant differences of sap flow between mean daytime and nighttime, between the wet season and the dry season, and of the contribution of nighttime water recharge to the total transpiration between dry and wet seasons. One-way ANOVA was used to test whether there were significant differences among the contribution of nighttime water recharge to the total transpiration at different DBH ranks.

The correlations between sap flow and the environmental factors in the dry and wet seasons, as well as the correlations between nighttime and daytime sap flow, were determined by Pearson's analysis. As for the possible factors affecting nighttime stem water storage ( $W_n$ ), multiple linear regressions between  $W_n$  and the environmental factors were performed.

Curve estimation analyses on the correlation between nighttime  $J_s$  and  $T_a$  VPD, as well as between  $W_n$  and tree characteristics were performed.

## RESULTS

### The diurnal, seasonal and inter-annual variation of nighttime sap flow

Fig. 2 illustrates the nighttime sap flow activities in both the dry (October to February) and wet seasons (March to September). Our observations indicated that sap flow was relatively higher and fluctuated more significantly before mid-

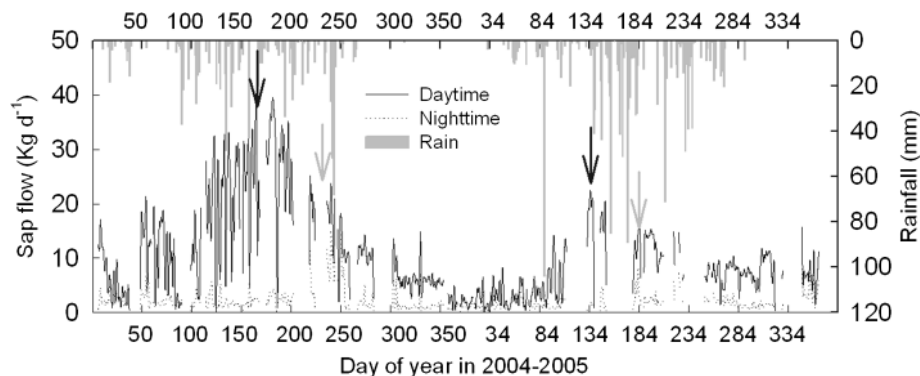
night, while after midnight it was approaching a steady state. It was also shown that sap flow after midnight was slightly higher in the dry season compared to that in the wet season, which is consistent with the higher demand of stem water recharge in the dry season.

Both daytime and nighttime mean sap flux densities of *A. mangium* increased in the wet season and went down in the dry season (Fig. 3). Although both of them had peak values in the wet season, nighttime sap flow was later than daytime sap flow (Fig. 3). Furthermore, both were significantly correlated with each other ( $r = 0.280$ ,  $n = 522$ ,  $P = 0.000 < 0.05$ ). There existed significant difference of sap flow between the wet and the dry season (for daytime sap flow,  $P = 0.000 < 0.05$  in both 2004 and 2005; for nighttime sap flow,  $P = 0.000 < 0.05$  in 2004,  $P = 0.012 < 0.05$  in 2005) (Fig. 4b and c).

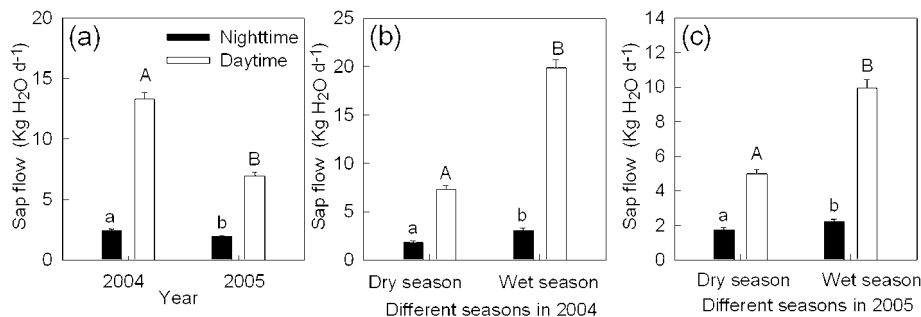
Both daytime and nighttime mean sap flow were higher in 2004 than in 2005 (Fig. 4a, daytime  $P = 0.000$ ; nighttime  $P = 0.003$ ), although rainfall was lower in 2004 (1122.4 mm) than in 2005 (1342.5 mm), adding that the  $T_a$  and PAR were similar in the 2 years ( $n = 694$ ,  $P = 0.466$ ,  $P = 0.117$ ).

### Environmental control of nighttime sap flow

Since radiation is absent during the nighttime, the interaction of environmental driving factors is different from that during the daytime. Correlations analyses on both daytime and



**Figure 3:** daytime and nighttime sap flow of *A. mangium*, as well as the rainfall in both 2004 and 2005. The black arrows pointed to peak values of daytime sap flow, while the gray arrows pointed to peak values of nighttime sap flow.



**Figure 4:** (a) mean daytime and nighttime sap flow of *A. mangium* in both 2004 and 2005. (b, c) mean daytime and nighttime sap flow of *A. mangium* in both the wet season and the dry season in both 2004 and 2005 (*t*-test,  $P < 0.05$ ).

nighttime sap flux density ( $J_s$ ) of *A. mangium* and  $T_a$ , VPD, SWC and  $v$  in the dry and wet seasons of 2005 were conducted and the results are shown in Table 1. Nighttime sap flow was significantly correlated with  $T_a$  in the dry season and with  $T_a$ , VPD,  $v$  in the wet season. Daytime sap flow was significantly correlated with  $T_a$ , VPD and SWC in the dry season and with  $T_a$  and VPD in the wet season.

Mean nighttime  $J_s$  corresponded closely to mean  $T_a$  at the study site. Regression analysis showed a significant correlation between nighttime  $J_s$  and  $T_a$ , but  $T_a$  did not adequately explain the variation in nighttime  $J_s$  ( $r^2 = 0.05$ ,  $r^2 = 0.11$ ) (Fig. 5a and b). The sensitivity of nighttime  $J_s$  to  $T_a$  in the dry and wet seasons ( $r^2 = 0.05$ ,  $P < 0.0001$ ;  $r^2 = 0.11$ ,  $P < 0.0001$ ) differed significantly from that of daytime  $J_s$  to  $T_a$  ( $r^2 = 0.39$ ,  $P < 0.0001$ ;  $r^2 = 0.39$ ,  $P < 0.0001$ ). Mean nighttime  $J_s$  also corresponded closely to nighttime VPD. However, the regressions describing the relationship of the two variables were significant in the wet season ( $P < 0.05$ ), but not in the dry season ( $P > 0.05$ ) (Fig. 5c and d). The sensitivity of nighttime  $J_s$  to VPD ( $r^2 = 0.0004$ ,  $P > 0.05$ ) was much lower than that of daytime  $J_s$  to VPD in the dry season ( $r^2 = 0.37$ ,  $P < 0.0001$ ), while they were more or less the same in the wet season ( $r^2 = 0.11$ ,  $P < 0.05$ ;  $r^2 = 0.07$ ,  $P < 0.05$ ) (Fig. 5c and d). The results presented above are consistent with the assumption that nighttime sap flow is principally allocated to the refilling of depleted water storages (Daley and Phillips, 2006).

### Nighttime leaf transpiration

There existed substantial nighttime leaf transpiration in the studied trees (Fig. 6) that decreased sharply after 17:00, slightly increased around midnight and then remained steady.

To provide a basis for estimating the amount of stored water, we compared temporal dynamics of nighttime  $J_s$  (measured with the TDP method) and possible nighttime transpiration rates of canopy leaves (measured with the gas exchange

method) in July 2006 as shown in Fig. 6. During the most nighttime, the  $J_s$  did not follow the changing trend of leaf transpiration. The total accumulated water loss ( $E_L$ ) by canopy leaves was only ~2.6–8.5% of the total nighttime sap flow ( $E_n$ ) (see the inserted bar graphic).

### Nighttime water recharge and its contribution to the total transpiration

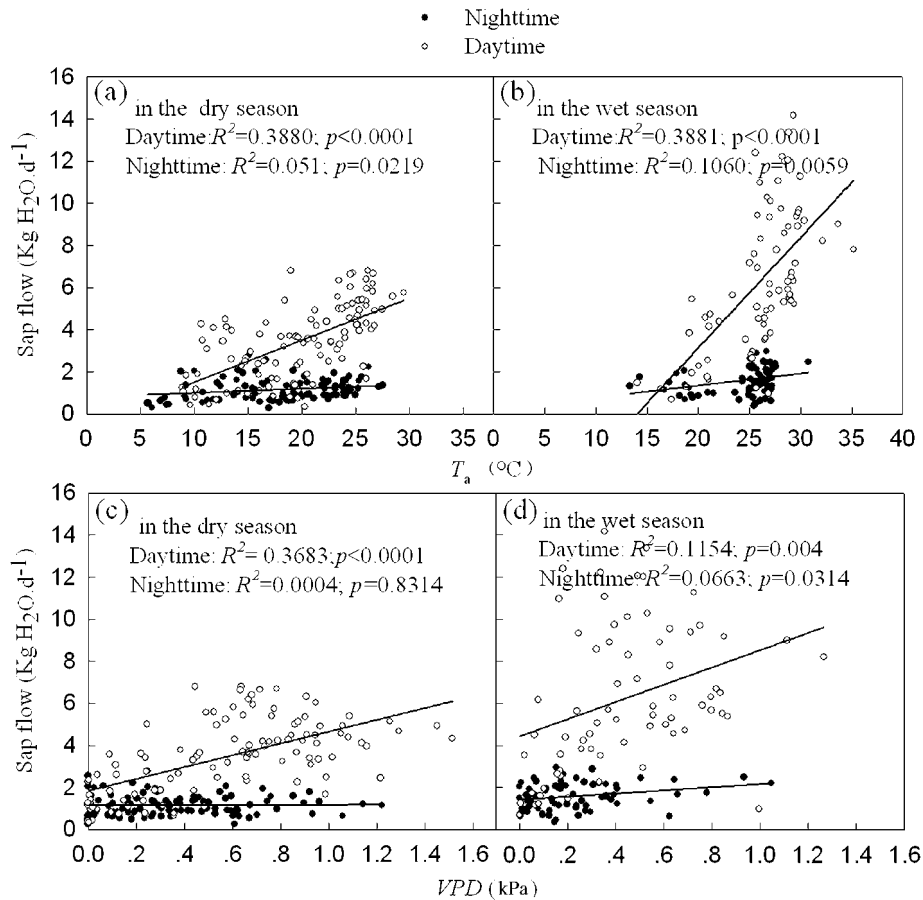
For nearly all 13 sample trees, nighttime water recharge in 2004 was higher than that in 2005 (Fig. 7a). Multiple regression models for the relationship between nighttime water recharge ( $W_n$ ) in *A. mangium* and SWC at the depth of 30 cm, air humidity (RH), air temperature ( $T_a$ ), as well as vapor pressure deficit (VPD, kPa) are shown in Table 2. Environmental factors can only explain limited amounts of nighttime stem water recharge. For example, the interaction of  $T_a$  and SWC explained 13% of the variation in  $W_n$  in 2004.  $T_a$  alone explained as little as 6% of the variation in  $W_n$  in 2005. The DBH, basal area and sapwood area explained more in regard to nighttime water recharge, accounting for 78, 81 and 81% in 2004 and 60, 60 and 60% in 2005, respectively. Moreover, the canopy size also could explain the variation in  $W_n$  to some degree accounting for 62 and 36% in 2004 and 2005, respectively. However, tree height and stem length below the branch could not explain the variation in  $W_n$  ( $P > 0.05$ ). Thus, DBH, basal area and sapwood area were the strong factors affecting  $W_n$  (Figs. 7b–g).

Our calculation showed that the contribution of nighttime stem water recharge to total transpiration of *A. mangium* ranged from 14.7 to 30.3% depending on different DBH classes and was considerably higher in the dry season compared to the wet season. In addition, the contribution of nighttime stem water recharge to total transpiration was higher in the trees with DBH ranging from 15 to 30 cm (Fig. 8).

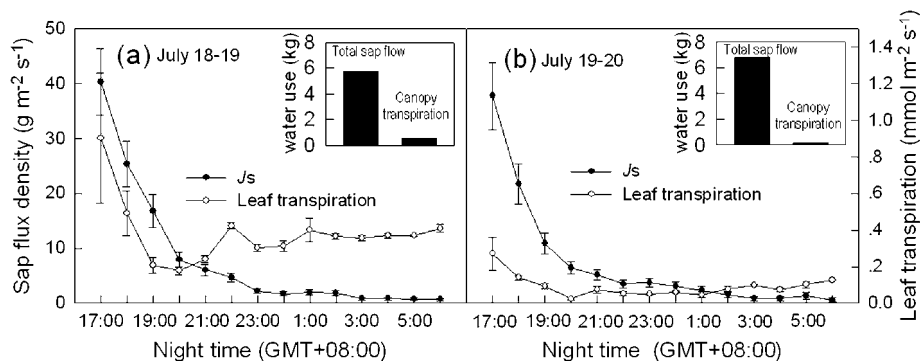
**Table 1:** correlations between both daytime and nighttime sap flux densities of *Acacia mangium* and air temperature ( $T_a$ ), vapor pressure deficit (VPD), soil water content (SWC) and wind speed ( $v$ ) in the dry and wet seasons of 2005

Sap flux density ( $\text{g m}^{-2} \text{s}^{-1}$ )		$T_a$ ( $^{\circ}\text{C}$ )	VPD (kPa)	SWC ( $\text{m}^3 \text{m}^{-3}$ )	$v$ ( $\text{m s}^{-1}$ )
nighttime in the dry season	Pearson correlation	0.267*	0.181	0.145	-0.083
	Significance (two tailed)	0.006	0.067	0.143	0.400
	$N$	104	104	104	104
nighttime in the wet season	Pearson correlation	0.334*	0.329*	-0.192	0.301*
	Significance (two tailed)	0.005	0.005	0.111	0.011
	$N$	70	70	70	70
Daytime in the dry season	Pearson correlation	0.556*	0.627*	-0.531*	-0.064
	Significance (two tailed)	0.000	0.000	0.000	0.511
	$N$	107	107	107	107
Daytime in the wet season	Pearson correlation	0.266*	0.618*	-0.014	-0.021
	Significance (two tailed)	0.022	0.000	0.905	0.860
	$N$	74	74	74	70

\*Correlation is significant at the 0.05 level (two tailed).



**Figure 5:** (a, b) sensitivity of sap flow to air temperature ( $T_a$ ) at night and during the day in 2005. The best fit linear relationship ( $y = a + bx$ ) for both daytime and nighttime. (c, d) sensitivity of sap flow to vapor pressure deficit (VPD) at night and during the day in 2005. The best fit linear relationship ( $y = a + bx$ ) for both daytime and nighttime.



**Figure 6:** dynamics of nighttime sap flux density and leaf transpiration rate of *A. mangium* during the nights of July 17–18 and 18–19, 2006.

## DISCUSSION

### Nighttime sap flow and its dependence on environmental factors

Our study revealed that nighttime sap flow of *A. mangium* was substantial and varied according to seasons and different times of the night (Figs 2 and 3). Nighttime sap flow correlated with daytime sap flow ( $r = 0.280$ ,  $n = 522$ ,  $P = 0.000 < 0.05$ ). This is

consistent with the results of Snyder's study (Snyder *et al.* 2003) which revealed that higher nighttime stomatal conductance and transpiration associated with higher daytime values across species and habitats, implying that quite an amount of nighttime sap flow was used to refill the stem water deficit as a result of high water loss during previous daytime.

It has previously been suggested that environmental factors, such as  $T_a$  and VPD, significantly affect nighttime sap flow

(Benyon 1999; Daley and Phillips 2006; Fisher *et al.* 2007; Hogg and Hurdle 1997). The significant correlation between some environmental factors and the nighttime sap flow of *A. mangium* observed in this study supports these findings (Table 1). However, environmental factors did not adequately explain the variation in nighttime sap flow (Fig. 5). Furthermore, nighttime sap flow in the dry season was less sensitive to environmental factors than in the wet season (Fig. 5), suggesting that the immediate and direct depletion of nighttime sap flow

**Table 2:** Multiple linear regressions between nocturnal water recharge ( $W_n$ ,  $\text{kg day}^{-1}$ ) and soil water content (SWC,  $\text{m}^3\cdot\text{m}^{-3}$ ), air relative humidity (RH, %), air temperature ( $T_a$ ,  $^{\circ}\text{C}$ ) and vapor pressure deficit (VPD, kPa)

Year	$n$	Equation	Adjusted $R^2$	$P$
2004	182	$W_n = 1.84 + 0.05 T_a - 0.03 \text{ SWC}$	0.13	<0.001
2005	119	$W_n = 0.29 + 0.06 T_a$	0.06	<0.01

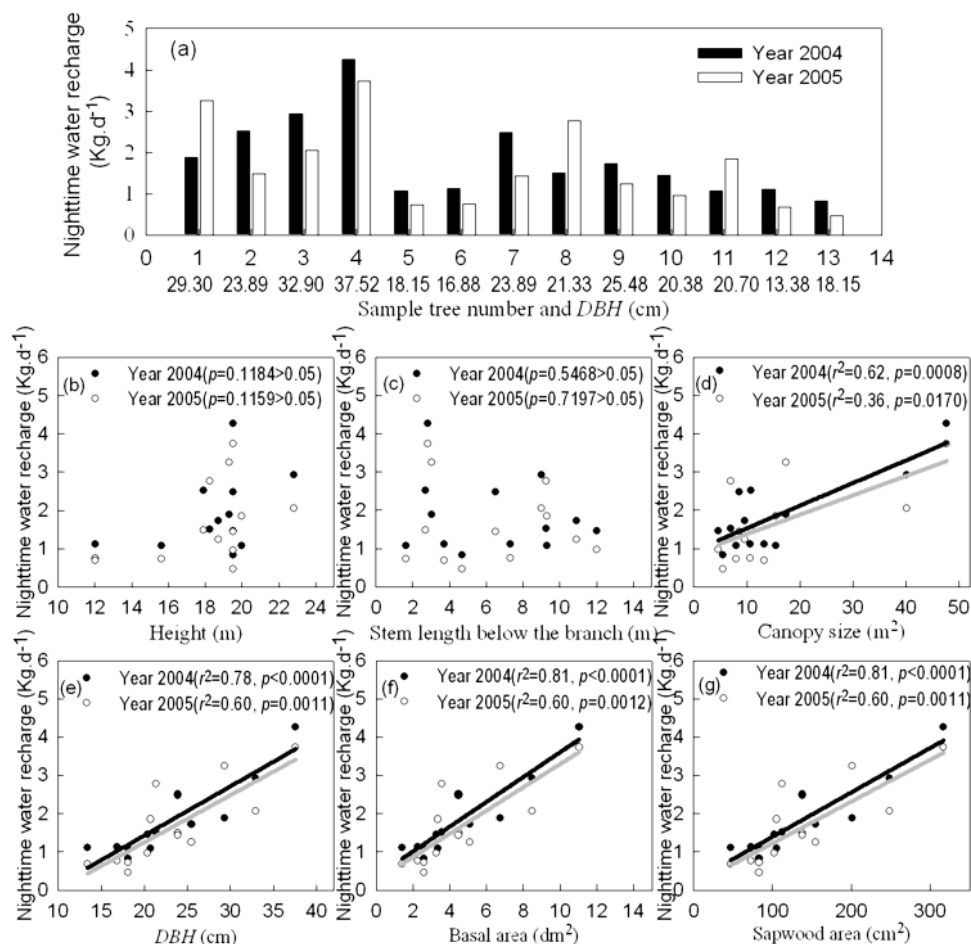
<sup>a</sup> For those regressions where the significant level was not reached, the related parameters and results, such as RH and VPD, were automatically eliminated.

by leaf transpiration of the canopy was minor. Another possible explanation may be that the growth rate of the examined stand was decreasing, for less vigorous physiological functions of the growth-recessing trees may mask the possibly significant nighttime transpiration of *A. mangium*. Limited information is available on how environmental factors influence nighttime sap flow seasonally. Our results show that the nighttime sap flow of *A. mangium* was chiefly influenced by  $T_a$  in the dry season, while it was predominantly influenced by the combination of  $T_a$  with VPD in the wet season (Fig. 5).

Both the nighttime and daytime sap flows were higher in the less precipitation year of 2004 but lower in the more precipitation year of 2005, which indicates that annual stand transpiration and the nighttime water recharge did not simply increase with increased annual rainfall (Figs 3 and 4).

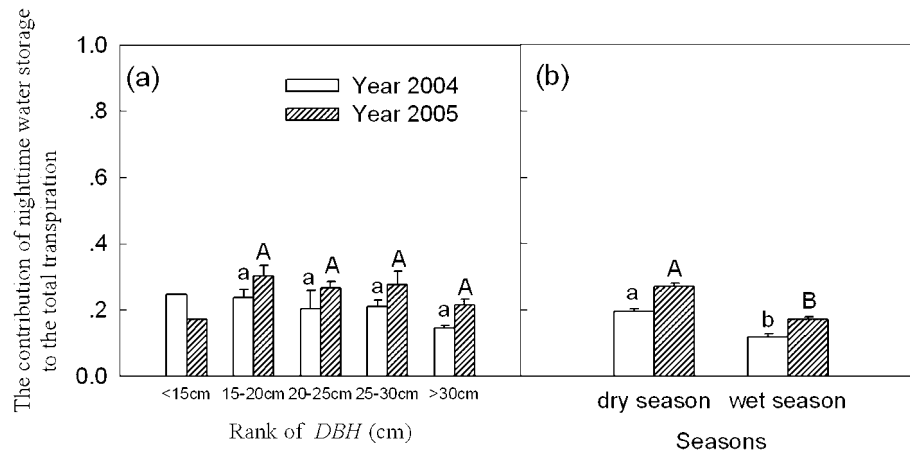
### Nighttime transpiration of leaves

It is commonly assumed that transpiration does not occur at night because leaf stomata are closed in the dark (Dawson *et al.* 2007). However, there is considerable evidence that stomata of some species do not completely close during the night (Benyon 1999; Daley and Phillips 2006; Snyder *et al.* 2003), which would



**Figure 7:** the nighttime water recharge of sample trees (a) and its regression relation with tree form features (b-g) in both 2004 and 2005.





**Figure 8:** the contribution of nighttime water recharge to the total transpiration of *A. mangium* at different DBH ranks in both dry and wet seasons in both 2004 and 2005.

allow for transpiration if there were sufficient environmental driving forces (Daley and Phillips 2006). In this study, slight nighttime transpiration was also observed in *A. mangium* (Fig. 6).

Leaf gas exchange and xylem sap flow measurements were conducted in order to investigate the partition of nighttime sap flow. We calculated the total accumulated water loss ( $E_L$ ) by transpiration of canopy leaves and compared it with the total nighttime sap flow ( $E_n$ ). It was found that the former was only ~2.6–8.5% of the latter (see the inserted bar graphic in Fig. 6). Therefore, it is likely that the nighttime sap flow we observed was mainly used for refilling water in the trunk. Contrary to our results, nocturnal sap flow was found to be primarily a function of transpiration from the canopy rather than refilling of stem storage, with canopy transpiration accounting for 50–70% of nocturnal flows in two co-occurring evergreen species (*Eucalyptus parramattensis* and *Angophora bakeri*) in a temperate woodland (Zeppel *et al.* 2010).

Notably, the accuracy of the upscaling method of transpiration estimation from leaf to canopy should be considered. The leaf gas exchange method gives accurate measurements of single leaf or twig, but the extrapolation to the canopy level is difficult because of the differences in boundary layers in cuvettes, light and humidity gradients within the crown, leaf age, growth stage and health condition (Schulze *et al.* 1985). To avoid these limitations and to minimize variation as much as possible, we chose more healthy leaves in the middle canopy to measure leaf transpiration. Thereby, the estimation of the total water loss from gas exchange was reasonable. Moreover, there existed large difference between transpiration and sap flow at night, which cannot be the results from the possible error by upscaling. Hence, our conclusion from the comparison was able to explain the function of nighttime sap flow.

### Nighttime water recharge and its implications for total transpiration

#### Nighttime water recharge and its affecting factors.

It is generally accepted that quantification of nighttime water refilling in sapwood requires the installation of multiple

sensors both at the base of the live crown and in the lower bole (Kavanagh *et al.* 2007). Although we did not strictly use this method to quantify the nighttime water-refilling, the slight allocation of nighttime sap flow to water loss by canopy transpiration provided us with the possibility to estimate nighttime water recharge by integrating the sap flux density over the time period of the whole night.

Plant size is often the major parameter determining water storage capacity (Goldstein *et al.* 1998). Total daily water use increases sharply with tree size ranging from 46 kg-day<sup>-1</sup> in the 0.34-m diameter individual of *Cordia alliodora* to 750 kg-day<sup>-1</sup> in the 0.98-m diameter individual of *Anacardium excelsum* (Meinzer *et al.* 2003). All five trees (*Cecropia longipes*, *A. excelsum*, *Ficus insipida*, *Luehea seemannii*, and *Spondias mombin*) conformed to common relationships between diurnal storage capacity and basal sapwood area, as well as tree height, suggesting that the relationships were species-independent and size-specific for trees of a seasonal tropical forest in Panama (Goldstein *et al.* 1998).

However, limited information on nighttime water recharge was available. In our study, the nighttime water recharge of *A. mangium* was strongly dependent on DBH, basal area and sapwood area (Fig. 8e–g). An alternative explanation may be that the nighttime recharge values were obtained by multiplying nighttime sap flux density by sapwood area calculated from DBH, which was consistent with that of Goldstein's study (Goldstein *et al.* 1998). Our results also showed the minor explanation capacity of the SWC and  $T_a$  to nighttime water recharge of *A. mangium* (Table 2), implying that leaf transpiration contribute little to the pulling force that drove the sap flow upward.

#### Implications of nighttime water recharge for the total transpiration.

The contribution of internal water storage to total daily water consumption varies widely, from 9 to 50% (Goldstein *et al.* 1998; Lostau *et al.* 1996; Waring *et al.* 1979). Since only part

of the stored water participates in the daily water use, recharging the water deficit can be considered as a contribution to total daily transpiration. Our estimates of nighttime water recharge contribution to the total transpiration ranged from 14.7 to 30.3% depending on different DBH classes in *A. mangium*, which are within the value range estimated for the other tree species mentioned above (Fig. 8a). The contribution of the internal water storage to daily transpirational loss was apparently not a fixed parameter in the water budget of trees (Goldstein et al. 1998). For example, the amount of water stored in the trunk of *Pinus pinaster* accounted for 12% of the daily transpiration in spring, but increased to 25% at the end of summer under drought conditions (Lostau et al. 1996). The magnitude of sapwood water storage of *Pinus sylvestris* ranges as high as 30–50% of the transpired water over periods of several days (Waring et al. 1979). Concordantly, the contribution of nighttime stem water recharge in *A. mangium* was higher in the dry season than in the wet season (Fig. 8b).

## CONCLUSION

Nighttime sap flow was significantly correlated with daytime sap flow in *A. mangium*. Environmental factors, although significantly affected nighttime sap flow, did not adequately explain the variation in nighttime sap flow of *A. mangium* at the daily scale, which may be due to the decreasing growth rates of the sample trees. The influence of environmental factors also varied with seasonal, daytime and nighttime dynamics. Slight nighttime leaf transpiration and incomplete closure of stomata were observed, which may be due to the fact that *A. mangium*, a tropical pioneer species, preferentially invests in high growth rates rather than water conservation. Our measurements and analyses suggest a greater allocation of nighttime sap flow to the refilling of depleted water storage. Nighttime water recharge was more strongly affected by tree features than by environmental factors at the daily scale. Its contribution to total transpiration loss changed with the seasons. Additional research is necessary to fully understand whether there may be insufficient time for completely refilling the tree sapwood before dawn. Furthermore, the error caused by nighttime water recharge on whole tree or stand transpiration deserves further investigation.

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